

Migration chronology of Eastern-Population Tundra Swans

S.A. Petrie and K.L. Wilcox

Abstract: We used satellite platform transmitting transmitters (PTTs) in 1998–2000 to track spring and fall migratory movements of Tundra Swans (*Cygnus columbianus columbianus*) captured at Long Point, Ontario. Migration corridors reported here corroborated those identified in previous studies using alphanumerically coded neck collars. However, PTTs provided additional information on duration of spring and fall migrations, duration of stay in different staging regions, time spent on breeding and wintering areas, and migration speed. Birds migrated between the Atlantic coast and northern prairies along a narrow geographic corridor through portions of the southern Great Lakes. From the northern prairies, swans followed 3 corridors to breeding areas on the west coast of Hudson Bay, central High Arctic, and Mackenzie River delta. While swans spent considerable time on Great Lakes (27% of spring migration) and northern prairie (40%) staging areas in spring, the northern boreal forest was an important fall staging area (48% of fall migration). Tundra Swans spent 20% of the annual cycle on wintering areas, 28% on spring staging areas, 29% on breeding areas, and 23% on fall staging areas. The long duration of migration and the fact that birds spend half their lives on staging areas underscore the importance of conserving Tundra Swan migratory habitats. Thirty-gram neck-collar-attached PTTs were more suitable than 95-g Teflon-harness-attached backpack PTTs for tracking Tundra Swans.

Résumé : L'utilisation d'émetteurs satellites (PTT) nous a permis de suivre les déplacements migratoires au printemps et à l'automne (1998–2000) de cygnes siffleurs (*Cygnus columbianus columbianus*) capturés à Long Point, Ontario. Les corridors de migration que nous avons identifiés confirment ceux qui ont été reconnus dans des études antérieures à l'aide de colliers munis de codes alpha-numériques. Cependant, les émetteurs PTT fournissent des données additionnelles sur la durée des migrations de printemps et d'automne, la longueur des séjours aux différentes stations de ralliement, le temps passé sur les sites de reproduction et d'hivernage, ainsi que la vitesse de migration. Les oiseaux se déplacent depuis la côte de l'Atlantique vers le nord des Prairies le long d'un étroit corridor géographique qui traverse des portions du sud des Grands Lacs. À partir du nord des Prairies, les cygnes suivent 3 corridors vers les aires de reproduction sur la côte occidentale de la Baie d'Hudson, dans le haut-Arctique central et dans le delta du Mackenzie. Alors que les cygnes passent beaucoup de temps sur les sites de ralliement de la région des Grands Lacs (27 % de la migration) et du nord des Prairies (40 %) au printemps, à l'automne, c'est le nord de la forêt boréale qui est l'important site de ralliement (48 % de la migration d'automne). Les cygnes siffleurs passent 20 % de leur cycle annuel dans les aires d'hiver, 28 % dans les sites de ralliement de printemps, 29 % dans les aires de reproduction et 23 % dans les sites de ralliement d'automne. La durée de la migration et le fait que les oiseaux passent la moitié de leur vie sur les sites de ralliement mettent en évidence la nécessité de conserver les habitats servant à la migration du cygne siffleur. Les émetteurs PTT de 30 g fixés à un collier cervical sont plus appropriés que les émetteurs fixés au dos par un harnais de téflon pour suivre les cygnes siffleurs.

[Traduit par la Rédaction]

Introduction

Eastern-Population (EP) Tundra Swans (*Cygnus columbianus columbianus*) migrate between Atlantic-coast wintering areas and Arctic-coastline breeding areas, which extend from Baffin Island to the North Slope of Alaska. Although previous neck-collar studies provided information about migration pathways of EP swans (Sladen 1973; Limpert et al. 1991), little is known about the chronology of migration during spring or fall.

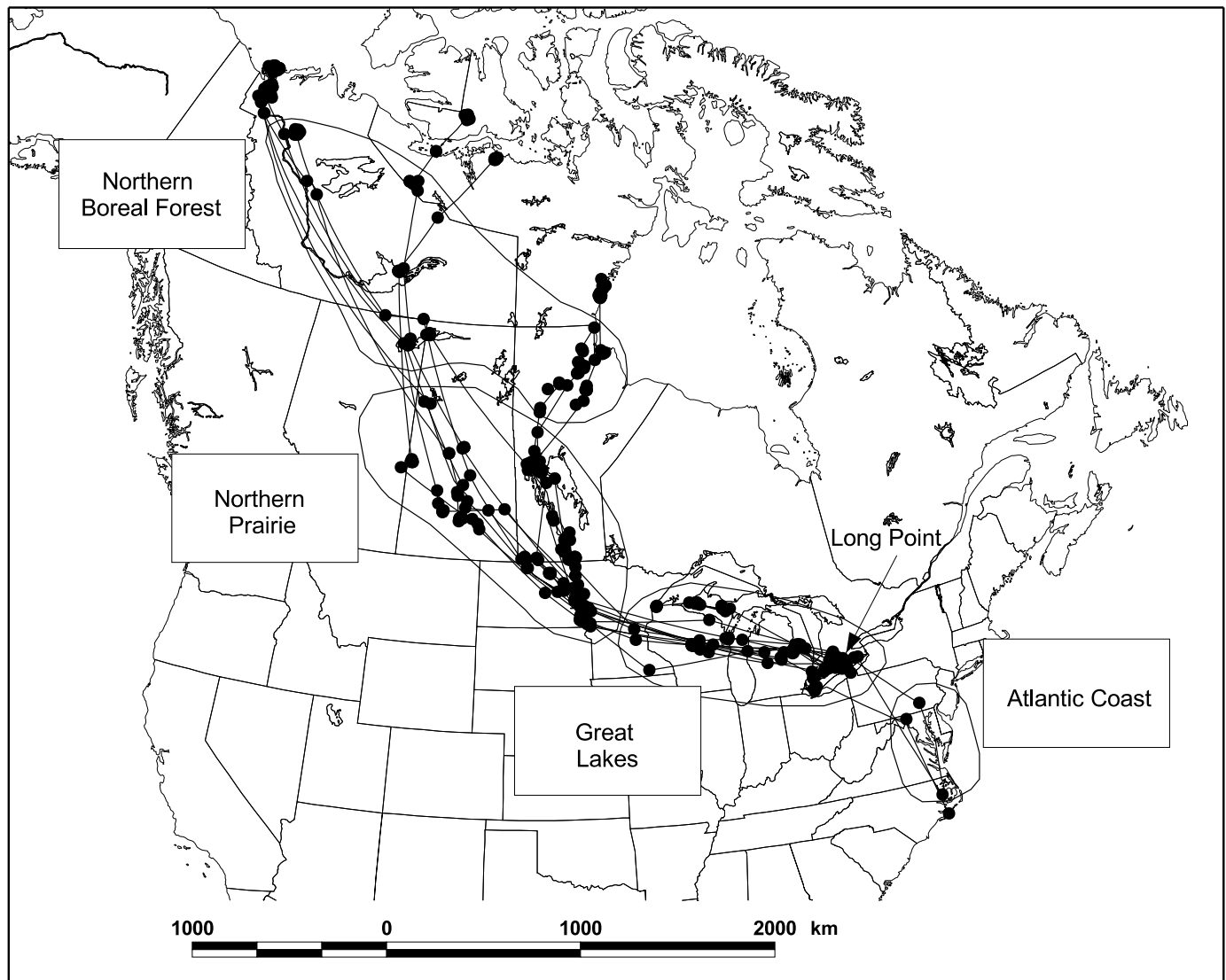
Migration is an important life-cycle stage for Tundra Swans. Tundra Swans arrive on Arctic breeding areas during spring thaw, when food availability is limited. Further, the Tundra Swan is one of the largest species of waterfowl in North America, and the cygnets grow and develop slowly (Bellrose 1980); the time required to raise cygnets to an age when they can migrate varies between 102 and 117 days (Bellrose 1980; McLaren and McLaren 1984; Hawkins 1986). These temporal and nutritional constraints likely dictate that Tundra Swans arrive on breeding areas with most of the nutrients necessary to lay and incubate a clutch of eggs (cf. Alisauskas and Ankney 1992), as egg laying is initiated soon after arrival. However, Tundra Swans lose body mass throughout winter and embark on spring migration with limited nutrient reserves (Bortner 1985; S.A. Petrie, unpublished data). Consequently, Tundra Swans must store reserves while they are incurring increased energetic costs associated with spring migration. Time constraints probably also dictate that juveniles continue to grow and acquire nutrient reserves during

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Fig. 1. Spring locations, migration routes, and breeding sites of PTT-marked Tundra Swans (*Cygnus columbianus columbianus*) tracked from southern Ontario ($n = 8$) and North Carolina ($n = 3$) in 1998–2000, identifying 4 important staging regions.



fall migration and that adults replenish reserves catabolized during reproduction and wing-feather replacement. Therefore, we suggest that the chronology of migration is probably influenced by nutrient-storage requirements of adults and growth requirements of juveniles.

Tundra Swan diets historically consisted primarily of submerged aquatic vegetation and to a lesser extent, benthic organisms (Stewart and Manning 1958; Sherwood 1960). Birds began feeding in agricultural fields in the 1960s, possibly in response to declines in availability of submerged aquatic vegetation at wintering and some migratory stopover sites, combined with uncharacteristically low winter temperatures (Nagel 1965; Tate and Tate 1966; Munro 1981). Whereas EP Tundra Swans now feed extensively in agricultural fields during winter (Bortner 1985) and spring (Petrie et al. 2002), they forage primarily in aquatic habitats during fall migration (Earnst 1994; Petrie et al. 2002). These differences in habitat use, combined with differences in nutrient requirements, may influence migratory patterns and cause

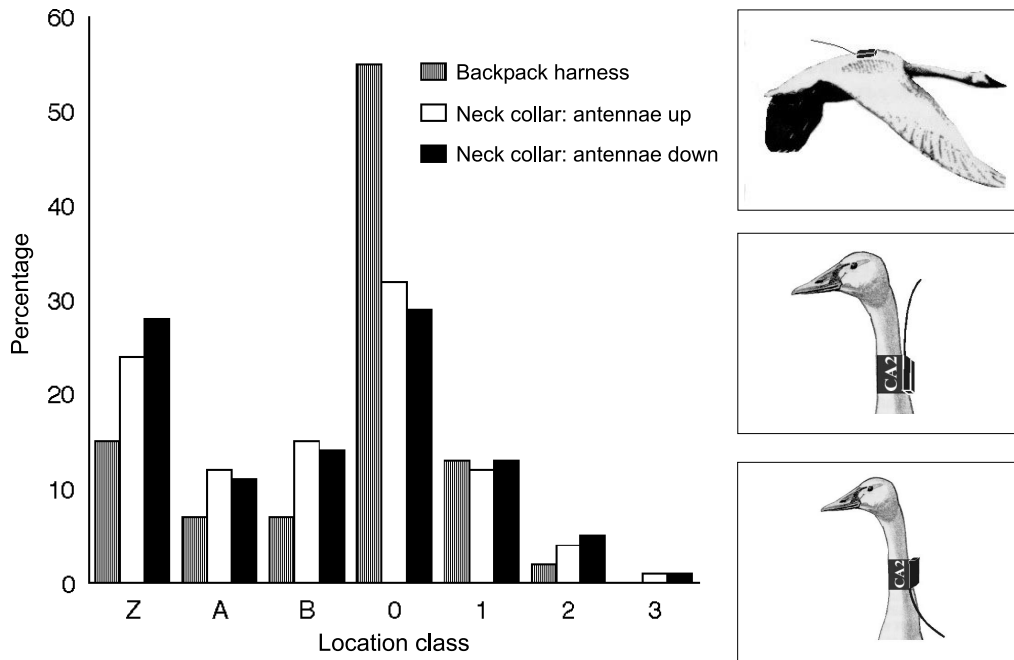
seasonal differences in staging areas used and (or) the duration of stay at those areas.

Here we present data from 12 Tundra Swans tracked from Long Point, Ontario, using satellite platform transmitting terminals (PTTs) (Argos 1996). Long Point is a suitable site from which to track swans because a major migratory corridor passes through southern Ontario (Sladen 1973), and mean peak fall counts (which provide a minimum estimate of swan use) at Long Point have increased from representing 0.7% of the EP in the 1970s to 7.9% in the 1990s (Petrie et al. 2002). We also report on observations of swans we neck-banded ($n = 62$) at Long Point. Our inferences about migratory movements and staging areas apply only to swans staging at Long Point.

Methods

Birds were captured in aquatic and terrestrial habitats in the vicinity of Long Point, which is a 35 km long sandspit

Fig. 2. Distribution of location classes (see Methods for definitions) received by 95-g backpack-harness-attached PTTs and 30-g neck-collar-attached PTTs (with antennae pointed up and down) used to track Tundra Swans in 1998–2000.



extending into the eastern basin of Lake Erie (42°35'N, 80°30'W to 42°33'N, 80°03'W) (Fig. 1). See Petrie (1998)² or Knapp and Petrie (1999) for a detailed habitat description.

Before harness-attached transmitters were deployed on free-ranging swans, we observed captive swans to ensure that the transmitter and attachment technique did not adversely affect the behavior, skin, or feathers, and that birds were not able to remove or destroy the transmitter. Two captive, flightless Tundra Swans were fitted with Teflon-harness-attached dummy PTTs and activity patterns were monitored during 144 ten-minute observation sessions distributed over a 4-week period during the winter of 1998. The activities of both members of the pair were recorded every 15 s during observation sessions. The number of instantaneous recordings of each activity for each bird was divided by the total number of recordings to obtain a percentage of time spent per activity. Transmitters were removed after 8 weeks, at which time birds were checked for feather wear and skin abrasion.

Tundra Swans were captured using rocket nets during spring and fall in 1998–2000 on Long Point's wetlands and neighboring agricultural fields. Sixty-two Tundra Swans (42 adults, 20 juveniles) were captured and equipped with black-and-white neck collars with alpha-numeric codes. Ten additional adult females and 2 adult males (not paired) were captured and equipped with PTTs. Four PTTs were attached in spring 1998, 3 in fall 1998, and 5 in spring 1999. Ninety-five-gram PTTs (Microwave Telemetry Inc., Columbia, Md.) were attached (backpack) to all 7 birds in 1998 using a Teflon harness attachment (Petrie et al. 1996). PTTs were programmed to transmit for 24 h/day for 30 days (to obtain information pertaining to macrohabitat use; see Petrie et al. 2002) followed by 8 h every 3 days. Theoretically, 95-g PTTs should last >2 years with this duty cycle. As all 7

PTTs operated <104 days, 30-g neck-collar-attached PTTs were used in 1999. These PTTs were riveted and epoxied to standard black-and-white neck collars by Microwave Telemetry, Inc.. To conserve battery life, these smaller transmitters were programmed to transmit for 8 h every 5 days. To determine whether orientation of the antennae influences location quality, collars were attached with the PTT antennae pointed upward ($n = 3$) and downward ($n = 2$) (Fig. 2). All work on captive and free-ranging Tundra Swans was performed under permit from the Canadian Wildlife Service and in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Birds' movements were monitored using the ARGOS satellite tracking system (Argos 1996). We subscribed to 3 data-processing products offered by Service Argos: Standard Processing, Auxiliary Location Processing, and 3-satellite service. Standard processing provided primary locations for PTTs when 4 or more signals were received during a satellite overflight and several data-processing criteria were met. Auxiliary Location Processing provided alternative locations for all Standard Processing criteria, including satellite overflights that only recovered 2 or 3 PTT transmissions. Service Argos reported that the accuracy of Standard Processing locations was generally within 1 km, and that use of location data from Auxiliary Location Processing was at the discretion of the investigator (Petersen et al. 1995). The 3-satellite service provided additional PTT locations by a third satellite.

We used both quantitative and qualitative criteria to remove aberrant locations typical of satellite tracking. First, we chose not to use Auxiliary Processing locations (Argos codes A, B, C, and Z), owing to limited confidence in their accuracy (Argos 1996). Then we selected one location from

²S.A. Petrie. 1998. Waterfowl and wetlands of Long Point Bay and Old Norfolk County: present conditions and future options for conservation. Unpublished report prepared for the Norfolk Land Stewardship Council.

Table 1. Relative performance of 30-g neck-collar-attached PTTs (antennae pointed up versus down) and 95-g backpack-harness-attached PTTs used to track Tundra Swans (*Cygnus columbianus columbianus*).

Transmitter type	<i>n</i>	Mean tracking duration (days)	Mean tracking distance (km)	Mean no. of locations
Neck collar				
Antennae up	3	218	6 534	462
Antennae down	2	350	11 690	497
Backpack harness	7	104	3 397	763

each primary/alternative pair, based on minimum distance from the previous location and rate of movement from the previous locations (Ely et al. 1997). Both locations were deleted if they did not meet our criteria. Our approach removed all locations that lacked reasonable biological plausibility unless they were validated by subsequent locations in the vicinity.

Because our satellite transmitters were programmed to transmit at different intervals, we used one satellite location per 24-h period for mapping purposes. This also reduced pseudo-replication. For instance, when there were several locations for a bird in a 24-h period, the best location class was selected. However, when a cluster of locations of the same accuracy were recorded, the central location was retained. Because duty cycles were programmed to conserve battery life, we were often unable to determine the exact date of departure from, or arrival on, staging, breeding and wintering areas. When this was the case, we assigned half of the days to the previous site and half to the new location. By programming transmitters to turn on every 3 or 5 days we may have missed some minor staging locations. Arcview was used to display the movements and an Animal Movement extension to Arcview (Hooze and Eichenlaub 1997) was used to calculate distances traveled.

Flight speed was calculated when numerous locations were received for individual birds that were known to be migrating, e.g., numerous locations were received along a relatively linear flight path. Only those locations obtained through Standard Processing (classes 0, 1, 2, and 3) were used and we limited our analysis of flight speed to instances when >2 h elapsed between initial and final locations and the distance traveled was >100 km.

Results

The captive male and female Tundra Swans spent 14.3 and 6.2%, respectively, of their time preening the harness and transmitter over the 4-week observation period. This compares favorably with results of other behavioral studies of captive birds with backpack transmitters (Perry 1981; Pietz et al. 1993; Petrie et al. 1996). Also, when transmitters were removed after 8 weeks, there were no obvious signs of feather wear, skin abrasion, or harness failure. Therefore, we felt justified in using harness-attached backpack transmitters to track the movements of free-ranging Tundra Swans.

Ninety-five-gram backpack-harness-attached PTTs provided 40% more locations than 30-g neck-collar-attached PTTs. This can be attributed primarily to differences in programmed transmission cycles (see Methods). Although backpack PTTs provided proportionately fewer class 1 and class 2 locations

than neck-collar-attached PTTs, they provided almost twice as many class 0 locations and fewer Z, A, and B locations (Fig. 2). However, neck-collar-attached PTTs operated longer (273%) and consequently tracked birds farther (268%) than backpack harness attachments (Table 1). Although sample sizes were small, orienting neck-collar-attached PTTs with the antennae downward did not adversely affect the quality of locations received (Fig. 2) or the operating period of the transmitter (Table 1). Results are based on two complete migrations (1 spring and 1 fall) and numerous partial migrations (10 spring and 6 fall) because PTTs were deployed on a staging area and the operational period of transmitters varied.

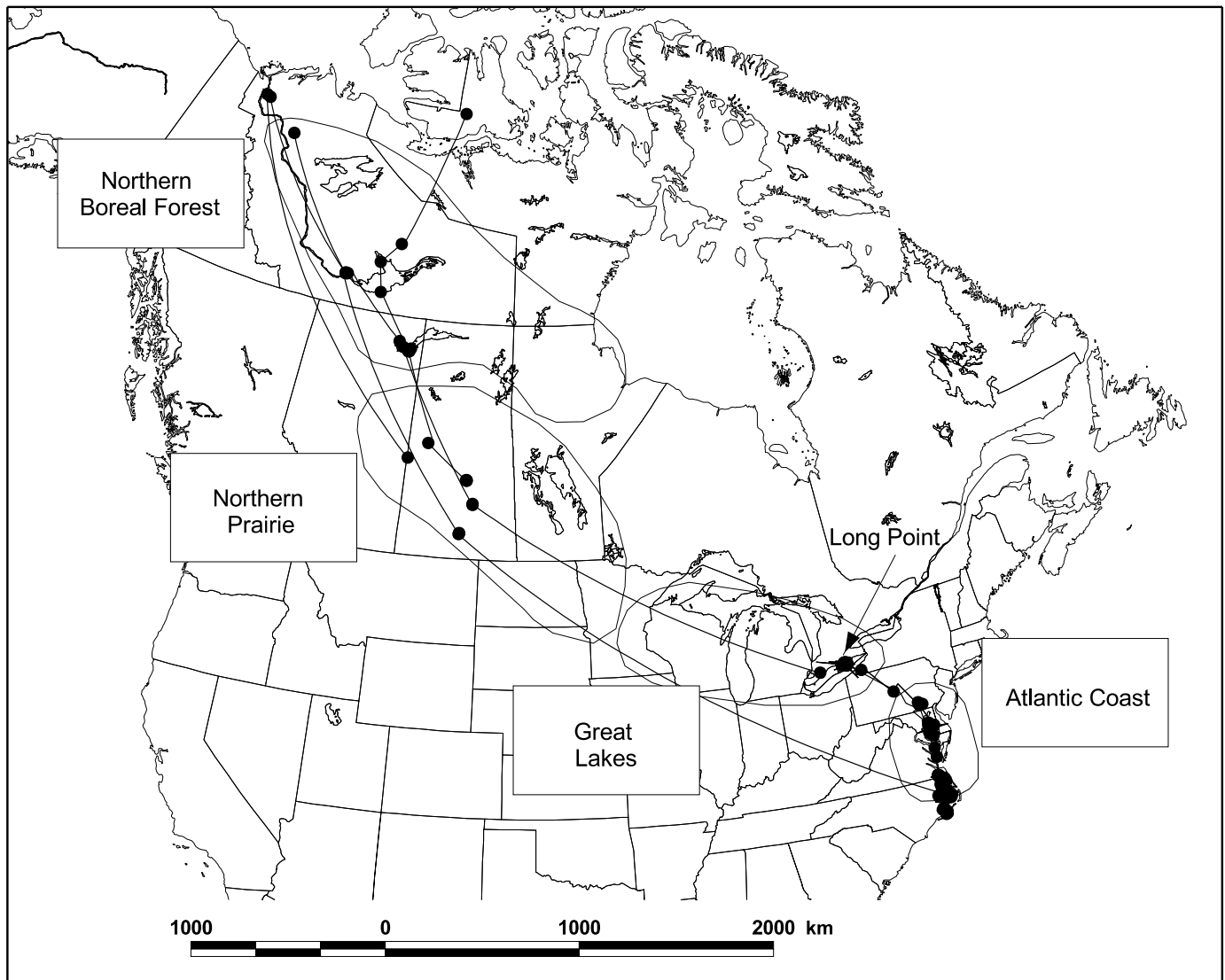
Spring migration

Spring migration results are based on 3 birds tracked from the Atlantic coast and 8 from Long Point. During the 3 years of study, the median date of departure from wintering areas was 17 February (range = 1–28 February, *n* = 3 swans) and the median date of arrival on breeding areas was 2 June (range = 11 May – 15 June, *n* = 8 swans). Based on the difference between median departure date from wintering areas (17 February) and median arrival date on breeding areas (2 June), spring migration lasts approximately 106 days. This is supported by the fact that one bird (20179) tracked throughout spring took 105 days to complete migration.

Swans used 4 distinct staging regions during migration: Atlantic coast, Great Lakes, northern prairies, and boreal forest (Fig. 1). After departing wintering areas, birds made 1–3 stops (\bar{x} = 1.7 stops) and spent 4–38 days (\bar{x} = 16 days) migrating between their southernmost wintering site and the lower Great Lakes. Brief stopovers were made along Chesapeake Bay and Delaware Bay, and one bird stopped for 2 weeks on the Susquehanna River, Md. Birds originally captured at Long Point spent 17–33 days (\bar{x} = 25 days, *n* = 3) in the Great Lakes region (southern Ontario, Michigan, and eastern Wisconsin), utilizing 3–6 different sites (\bar{x} = 3.7 sites), the most important being Long Point, Ont., Aylmer Wildlife Management Area, Ont., Lake St. Clair, Ont., Grand Bend, Ont., Saginaw Bay, Mich., coastal wetlands along the eastern shores of Lake Michigan, and Green Bay, Wis. When data were included for birds in the year they were captured at Long Point (unknown duration of staging before capture), the mean duration of staging only dropped to 21 days (range = 13–33 days, *n* = 11).

All birds left the Great Lakes in late March or early April and traveled west to the northern prairies (western Minnesota, northeastern North Dakota, and southern Manitoba and Saskatchewan) (Fig. 1). Birds spent 25–45 days (\bar{x} = 37 days, *n* = 11) in the northern prairies and utilized 2–6 different

Fig. 3. Fall locations and migration routes of PTT-equipped Tundra Swans tracked from Long Point ($n = 3$) and the Canadian Arctic ($n = 5$) in 1998–2000.



sites ($\bar{x} = 4$ sites, $n = 11$). After leaving the northern prairies, birds traveled to the northern boreal forest (northern Manitoba, Saskatchewan, and Alberta, northwestern Northwest Territories (N.W.T.), and western Nunavut). Birds spent 3–32 days ($\bar{x} = 14$ days, $n = 9$) in the boreal forest region and utilized 1–3 different sites ($\bar{x} = 1.6$ sites, $n = 9$). Important staging areas were Lake Athabasca, Alta., Churchill River, Man., Southern Indian Lake, Man., Great Slave Lake, N.W.T., and the Mackenzie River and upper Mackenzie River delta, N.W.T.

Although swans migrated along a single narrow corridor across the southern Great Lakes, 3 different migration routes were taken north from the northern prairie region: one route to the west coast of Hudson Bay (swans 3687, 3688, 3641), a second route to the central arctic (swans 20112, 20180), and a third route to the Mackenzie River delta (swans 20114, 3743, 20179 (2 times), 20113). The total migration distance (one way) for one bird (20179) that wintered in North Carolina and bred on the Mackenzie River delta was 5897 km. Tracked birds spent the summer on the west coast of Hudson Bay,

Victoria Island, Queen Maud Gulf, Mackenzie River, and the Mackenzie River delta (Fig. 1). The median arrival date on breeding areas was 2 June (range = 11 May – 15 June, $n = 8$) and the median departure date was 11 September (range = 24 August – 28 September, $n = 4$). Four birds tracked throughout the summer remained on nesting/brood-rearing areas for 76, 96, 112, and 140 days ($\bar{x} = 106$ days).

Autumn migration

Fall migration results are based on 4 birds tracked from breeding areas and 3 from Long Point (Fig. 3). The median departure date from breeding/molting areas was 11 September (range = 24 August – 28 September, $n = 4$) and the median arrival date on Chesapeake Bay was 3 December (range = 5 November – 31 December, $n = 4$). The difference between median departure date from the breeding/molting area (11 September) and arrival date on the wintering area (3 December) suggests that fall migration lasts approximately 84 days. The one bird (20179) we tracked throughout fall took 73 days to migrate, but the short time spent on the breeding area and

its migration speed (2864 km within 4 days) suggest that this bird did not breed successfully and so was not migrating with cygnets.

After leaving breeding areas, birds spent considerable time in the northern boreal forest region (\bar{x} = 41 days, range = 32–49 days; n = 4). The 3 most important staging areas were the upper Mackenzie River delta, Great Slave Lake, and Lake Athabasca. The median arrival date in the northern prairies was 29 October (range = 17 October – 7 November, n = 3) and the median departure date was 21 November (range = 3–28 November, n = 3). Birds spent 18–24 days (\bar{x} = 21 days, n = 3) in the prairies and utilized 1–2 different sites (\bar{x} = 1.3 sites). Lakes in south-central Saskatchewan were the primary fall staging sites of the 3 tracked birds. Bird 20179 was in southern Saskatchewan on 31 October 1999 and was subsequently recorded in North Carolina on 5 November. While the exact route is unknown, this bird migrated at least 2845 km within 4 days and spent little or no time in the lower Great Lakes region during fall migration. Another bird (20114) that was tracked from the northern prairies arrived in southern Ontario on 5 December before its transmitter failed. Three birds marked at Long Point during fall 1998 remained for 11–17 days (\bar{x} = 13 days), but it is not known how long these birds were at Long Point before being captured. Using the difference between mean duration of fall migration (84 days) and mean duration of stay in the boreal forest (41 days) and northern prairies (21 days), we estimate that birds remained in the lower Great Lakes for approximately 22 days during fall. However, there may be substantial individual and annual variation in amount of time birds remain in each of the 3 regions and inferences from our results apply only to individuals captured at Long Point. With the exception of 1 bird stopping in western New York State for 1 day, all 3 birds leaving southern Ontario migrated directly to northern Chesapeake Bay.

Winter

Of 4 birds tracked to Atlantic-coast wintering areas, initial arrival locations could be determined for 3, which all arrived at the north end of Chesapeake Bay, near Baltimore, Md. (Fig. 3). The median day of arrival on Chesapeake Bay was 3 December (range = 5 November – 31 December, n = 4). From Maryland, birds traveled south along Chesapeake Bay, arriving in the Lake Mattamuskeet and (or) Pamlico Sound regions of North Carolina a few days to a few weeks later. Birds tended to make several stops (\bar{x} = 6 stops) along Chesapeake Bay during this southward movement. Time spent on Chesapeake Bay during winter varied from 47 to 104 days (\bar{x} = 72 days, n = 3 birds); the median departure date from the southernmost Atlantic-coast wintering areas was 17 February (range = 1–28 February, n = 3).

Observation data

Of 62 neck-collared Tundra Swans, 41 observations of 29 birds were made (a 47% resighting rate). Two birds were shot during the hunting season in North Dakota and 5 were shot in North Carolina (Fig. 4). All observations of neck-collared Tundra Swans were made on wintering areas or in the southern half of the migratory range (Fig. 4). One notable exception to the pathways taken by satellite-tracked birds

was one bird that was observed in California (within the range of the Western Population (WP)).

Flight speed

Estimates of flight speed ranged from 37 to 70 km/h (\bar{x} = 48 km/h, SE = 3.2 km/h; n = 12) in spring and from 48 to 59 km/h (\bar{x} = 54 km/h, SE = 3.3 km/h; n = 3) in fall. Based on mean calculated flight speed, total flight time would be approximately 114 h in spring and 101 h in fall for birds migrating between Pamlico Sound, North Carolina, and the Mackenzie River delta, N.W.T.

Discussion

Migration corridors used by satellite-tracked and neck-banded Tundra Swans corroborated those identified in previous studies using alphanumerically coded neck collars (Sladen 1973). However, satellite-tracked PTTs provided additional information on the duration of spring and fall migration, duration of stay in different staging regions, time spent on breeding and wintering areas, movement patterns on breeding and wintering areas, and migration speed.

Transmitter performance

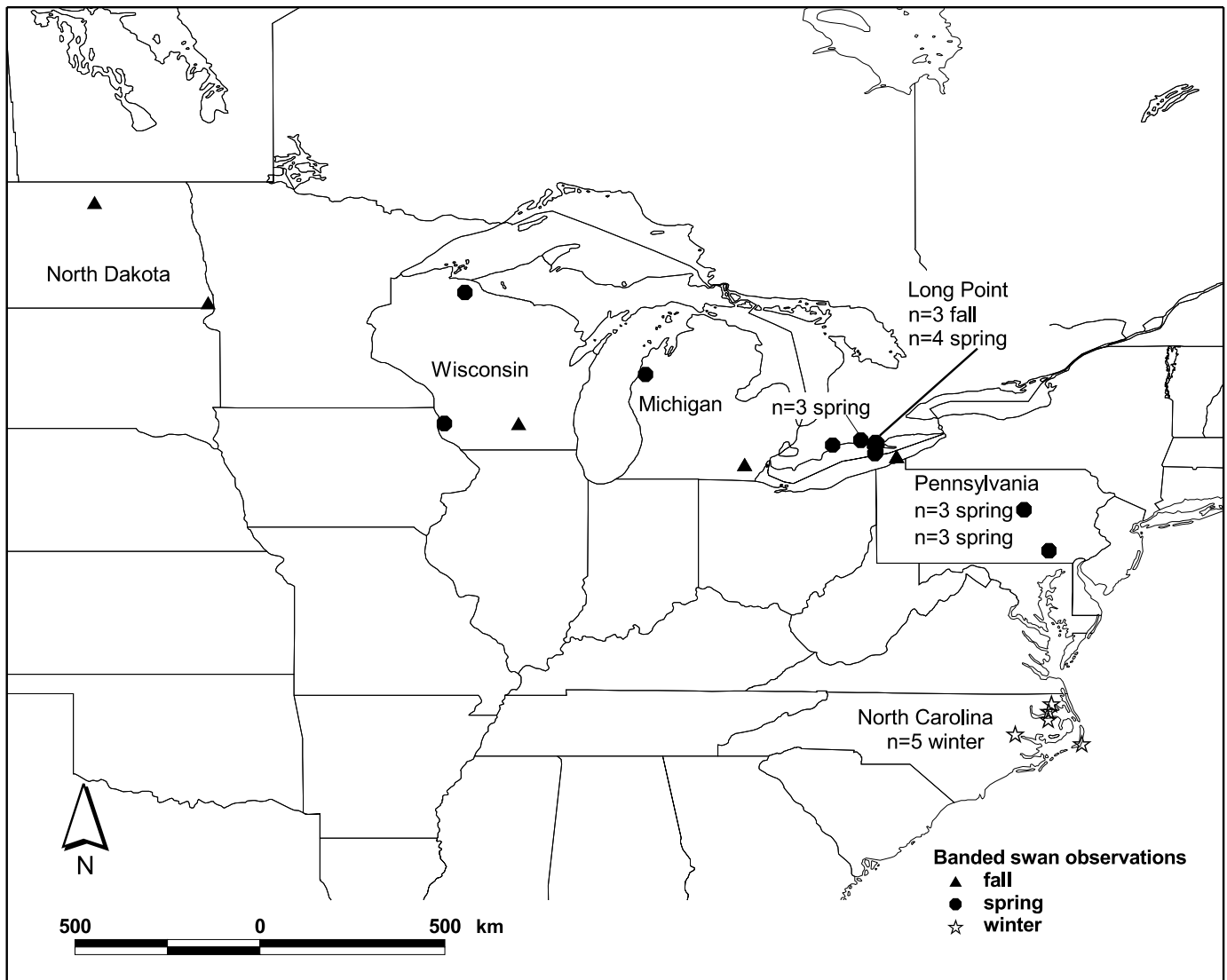
Work on captive birds suggested that backpack-harness-attached transmitters do not adversely affect the behavior, skin, or feathers of flightless Tundra Swans, and birds were unable to remove the transmitters during 8 weeks of wear. However, despite 95-g backpack-harness-attached transmitters having a life expectancy of >2 years, mean tracking duration was only 104 days. Early failure can be attributed to some combination of transmitter failure, bird death, and transmitters falling off birds. Regardless of the reason, we found backpack-harness-attached PTTs to be unreliable and not a cost-effective method of tracking Tundra Swans for extended periods.

The 30-g PTTs had a life expectancy of nearly 1 year. They continued to transmit for an average of 218 days (one continued to transmit for 581 days), suggesting that neck-collar attachments are more suitable for tracking Tundra Swans. Neck-collar-attached PTTs were also easier to attach and quicker to deploy, probably resulting in less stress to the bird. Further, affixing PTTs with the antennae orientated downward did not adversely affect the quality of locations received, is probably less invasive to the bird, and would reduce drag during flight. However, because waterfowl hunters sometimes select birds with noticeable external attachments, we suggest that researchers attach PTTs to white collars, as these are less conspicuous.

Spring migration

Tundra Swans departed Atlantic-coast wintering areas during February and arrived on breeding areas between mid-May and mid-June. Therefore, spring migration lasted over 100 days, despite the estimated flight time required to complete migration being only about 114 h. Early departure from wintering areas may be a function of food depletion on wintering areas and the ready availability of waste agricultural grains and new-growth winter wheat on spring staging areas. The long duration of spring migration also may be influenced by the need for adults to arrive on breeding grounds

Fig. 4. Distribution of fall, spring, and winter observations of neck-collared Tundra Swans ($n = 62$) marked at Long Point, Ontario, in 1998–2002, excluding one recovery in California and within-season and within-location multiple resightings of individual swans.



with ample reserves for reproduction and the fact that migration speed is limited by the availability of ice-free areas as birds travel northward.

Tundra Swans lose body mass throughout winter (Bortner 1985) and are still in relatively poor condition when they arrive in southern Ontario in early March (S.A. Petrie, unpublished data). Beekman et al. (1996) calculated that Bewick's Swans (*Cygnus columbianus bewickii*) had a maximum potential flight range of 1450 km and that stopover periods would need to last at least 2 weeks to allow them to replenish nutrient reserves completely. The distance between wintering areas in North Carolina and southern Ontario is approximately 1000 km, with an additional 1500 km to the northern prairie staging region. Therefore, the time spent consuming waste corn and submerged aquatic plants in the lower Great Lakes region (Petrie et al. 2002; S. Badzinski, unpublished data) would enable birds to acquire the nutrients necessary for them to continue migrating to the northern prairies.

Swans arrived in the northern prairies in late March and early April and spent considerable time (overall $\bar{x} = 37$ days;

$n = 11$) staging in western Minnesota, the Sheyanni National Grassland near Fargo, N.D., northeastern North Dakota, southern Manitoba, Moose Lake, Man., southern Saskatchewan, and Prince Albert National Park, Sask. The amount of time spent in this region combined with the need to arrive on breeding areas with ample reproductive reserves, and the fact that birds still have between 900 km (the western shores of Hudson Bay) and 2000 km (the Mackenzie River delta) left to migrate, suggest that birds probably acquire substantial endogenous reserves for continued migration and for reproduction while in the northern prairies.

After leaving the northern prairies, swans spent only an average of 14 days in the northern boreal forest before flying to breeding areas. This is only 15% of the time spent on staging areas during spring migration, as opposed to 40% of migration in the northern prairies and 27% in the Great Lakes. Therefore, Tundra Swans spent relatively more time in southern staging regions during spring. This is probably due to the limited availability (winter senescence) and accessibility (ice cover) of submerged aquatic plants in the

northern boreal forest in spring, and the availability of waste grains in Great Lakes and northern prairie landscapes during that time. Further, we hypothesize that Tundra Swans arrive in the northern boreal forest with sufficient nutrient stores for reproduction, and that they remain in the boreal forest only as long as weather conditions prevent them from completing migration.

Summer movements

Swans captured at Long Point bred on the western shores of Hudson Bay, Victoria Island, Queen Maud Gulf, Mackenzie River, and the Mackenzie River delta. Birds arrived on breeding areas between mid-May and mid-June and departed between late August and late September. Total time spent on or near breeding areas was 76–140 days (\bar{x} = 106 days). As it takes 102–117 days to raise cygnets to an age at which they can successfully migrate (Bellrose 1980; McLaren and McLaren 1984; Hawkins 1986), the variability in time spent on and near breeding areas is probably due to early departure of nonbreeders and unsuccessful breeders from breeding areas.

Bird 20114 arrived on the Mackenzie River, N.W.T., remained in the general area for 140 days, and did not appear to move between a distinctive nesting site and a brood-rearing site. Similarly, bird 20180 arrived at an inland site on Victoria Island, remained for 112 days, and did not change locations during that time. Conversely, after spending 21 days in 1999 and 38 days in 2000 on Richards Island in the Mackenzie River delta, bird 20179 moved 39 and 61 km to the east, where it remained for 59 and 58 days, respectively. Since territorial adults, especially those with cygnets, tend to remain on territories until they finish wing-molting in late summer (Earnst 1992; Limpert and Earnst 1994), birds 20114 and 20180 likely held breeding territories, whereas 20179 probably did not hold a breeding territory or failed early in its breeding attempt during 1999 and 2000, and subsequently relocated before wing molt.

Fall migration

Fall migration took about 1 month less than spring migration, despite juveniles being younger in fall. This may be due to birds being driven south by advancing winter conditions in fall and delayed by ice cover in spring. Whereas birds spent limited time in the northern boreal forest region in spring, all birds spent long periods there in fall (32–49 days). Relative to spring, the availability of submerged aquatic vegetation in boreal-forest wetlands would be higher in fall, after the summer growing period. Tundra Swans fledge at a smaller proportion of adult mass than do geese and are still growing when they depart breeding areas (Bellrose 1980; Sedinger 1992). Therefore, the increased time spent in the northern boreal forest in fall is also consistent with the continued growth requirements and limited stamina of juveniles, and possibly the need for adults to replenish nutrients catabolized during reproduction and wing-feather replacement.

In contrast, WP Tundra Swans spend only a few days in northern areas before migrating to central Alberta (Ely et al. 1997). Differences in duration of stay in northern staging areas between WP and EP swans are probably due to fundamental differences in the suitability of breeding habitats. WP

swans breed between latitudes 57 and 65°N, whereas EP swans breed between latitudes 68 and 72°N. Mean daily temperatures in May and September in the Rasmussen lowlands (an important EP breeding area) are –10.1 and –1.1°C, respectively, (Atmospheric Environment Service 1982), whereas temperatures on the Yukon–Kuskokwim delta (an important WP breeding area) at that time average about 2 and 6–8°C, respectively (Brower et al. 1977). Consequently, WP swans generally arrive on Yukon–Kuskokwim delta breeding areas 3 weeks earlier than EP swans arrive in the Northeastern Keewatin District, Nunavut (Lensink 1973; McLaren and McLaren 1984). Accordingly, peak hatch on the Yukon–Kuskokwim delta begins between 20 June and 6 July (Lensink 1973), whereas peak hatch in the Rasmussen lowlands does not occur until after 10 July (McLaren and McLaren 1984). Ely et al. (1997) reported that satellite-tracked WP swans initiated migration in late September, whereas EP birds tracked in this study initiated migration from 24 August to 28 September, despite the fact that EP swans hatch later. Therefore, the increased time spent in northern boreal forest regions by EP swans is probably a function of birds being forced by cold weather to leave breeding areas earlier than WP birds; also, EP cygnets, being hatched later, are likely less capable of enduring sustained flights in early fall.

Upon leaving the northern boreal forest, 3 tracked swans staged on large wetlands in central and southern Saskatchewan. Use of large wetlands at that time can be attributed to birds foraging primarily on submerged aquatic plants during fall migration (see Earnst 1994; Petrie et al. 2002). Birds spent somewhat less time in the northern prairie region during fall migration (\bar{x} = 21 days) than during spring (\bar{x} = 37 days), but our fall sample size was very small.

Upon leaving the northern prairie region, both tracked birds made extensive movements, one to North Carolina within 4 days (2895 km, bird 20179) and the other to southern Ontario within 4 days (2085 km, bird 20114) (Fig. 3). Breeding-ground movements suggest that 20179 did not breed successfully, and migrating without cygnets may have enabled this bird to make such an extensive move. However, there is some evidence that Tundra Swans travel longer distances between staging areas in fall than in spring (Sladen et al. 1969). We estimate that Tundra Swans that stop in southern Ontario in fall do so for approximately 3 weeks. Large numbers of EP swans also stage on the Upper Mississippi River in fall for approximately 1 month (Thorson et al. 2002). The amount of time spent on the lower Great Lakes and Upper Mississippi River in fall is probably dictated primarily by weather, as birds are in good condition upon arrival (S.A. Petrie, unpublished data from the lower Great Lakes), which reduces their need to linger and store nutrients. Also, there is no apparent advantage to early arrival on wintering areas.

Although Maryland was traditionally the primary wintering area of EP Tundra Swans, approximately 70% of the population now winters in North Carolina (Stewart and Manning 1958; Serie et al. 2002). With the exception of one bird (20179) that traveled from southern Saskatchewan to North Carolina within 4 days (exact route unknown), birds migrated almost directly from southern Ontario to northern Chesapeake Bay. From Maryland, birds made numerous stops as they migrated south to North Carolina. Therefore, most

birds use a series of staging/wintering areas as they move south along Chesapeake Bay. WP Tundra Swans show a similar pattern, with the number of birds in the Sacramento Valley decreasing as winter progresses, whereas swan use gradually increases on the San Joaquin delta to the south (Schroeder 1983;³ Heitmeyer et al. 1989).

Neck-collar observations and returns were within the migratory path identified by PTT-equipped birds. However, one bird was observed in California, which supports previous evidence that there is some mixing between EP and WP swans (Limpert et al. 1991). Our estimated flight speeds (range = 37–70 km/h) were less than those reported for WP swans (maximum speed = 60–90 km/h; Ely et al. 1997), which may be due to differences in weather patterns or to the presence or absence of cygnets.

Conclusions

(i) While Tundra Swans tend to use similar migratory pathways during spring and fall, there are seasonal differences in the staging areas that they use, as well as in time spent in each of the regions. (ii) The chronology of spring and fall migration is probably influenced by the use of agricultural grains, seasonal differences in the availability of submerged aquatic vegetation on staging areas, the need to arrive on breeding areas with ample reproductive reserves, and the growth requirements and stamina of juveniles. (iii) Conservation of staging habitats is critical, as EP swans spend half their life migrating between Atlantic-coast wintering areas and Arctic breeding areas. (iv) Thirty-gram neck-collar-attached PTTs were more effective than 95-g backpack-harness-attached PTTs for monitoring long-distance movements of Tundra Swans.

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